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# Natural history collections help resurrecting *Glomeris herzogowinensis* Verhoeff, 1898 and further clarify the nomenclature of two *Onychoglomeris* subspecies of Attems (Diplopoda, Glomerida, Glomeridae)

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## Abstract

Based on the study of freshly-collected material and old museum specimens, we have solved a decades-old riddle surrounding the name *Onychoglomeris herzogowinensis* (Verhoeff, 1898). The southern Dinaric coastal species *Glomeris herzogowinensis* Verhoeff, 1898 is revived, while *Onychoglomeris herzogowinensis australis* Attems, 1935 and *O. h. media* Attems, 1935, are treated here as full species after returning the specific name to *Glomeris* Latreille, 1902, *O. australis* Attems, 1935, **stat. nov.** and *O. media* Attems, 1935, **stat. nov.** Besides the designation of lectotypes, we provide comprehensive illustrations, diagnoses, detailed remarks and a distribution map for all three species. In addition, DNA barcoding provided COI sequences for *Glomeris herzogowinensis* and *Onychoglomeris australis* **stat. nov.**, along with the first barcoding data of one additional species of *Onychoglomeris* Verhoeff, 1906, *O. ferraniensis* Verhoeff, 1909 and two *Glomeris* species, the Balkan *G. balcanica* Verhoeff, 1906 and the trans-Adriatic *G. pulchra* Koch, 1847. The significance of historical specimens from natural history museums is briefly discussed.

## Key Words

Balkan Peninsula, COI, Europe, Glomerinae, lectotype, syntypes, taxonomy

## Introduction

The Western Palaearctic genus *Glomeris* Latreille, 1802 comprises about 75 species with a smaller number of taxa in the Canary Islands, North Africa and Anatolia and the majority of species on the European continent (Enghoff et al. 2015). Apart from the fact that this genus includes some of the most attractive and colourful millipedes in Europe, it is certainly a nightmare for taxonomists. Around 60 species of the genus live on the continent today, with an unfathomably large number of subspecies, varieties, forms or morphs having been described in the past, counted in hundreds (Golovatch et al. 2009). It is interesting to note that more than 80 forms have been described within the common central and southeast European species *Glomeris hexasticha* Brandt, 1833 alone (Kime and Enghoff 2011). Due to insufficient taxonomic information on the structure of the telopods and their uniformity in this group, the species, subspecies or "lower categories" are mostly described on the basis of colour patterns. While in some species this pattern may be stable, in many others, there is variability, even within the same population, where the colouration of one species may be similar or identical to the colour pattern of an-

other species. Fortunately, the chaotic situation within the genus and the order Glomerida, in general, has improved somewhat in recent decades, largely due to an integrative approach to the problem (Hoess et al. 1997; Hoess and Scholl 1999a, 1999b, 2001; Hoess 2000; Oeyen and Wesener 2015; Wesener 2015a, 2015b, 2018; Wilbrandt et al. 2015; Wesener and Conrad 2016; Reip and Wesener 2018; Antić et al. 2021).

One of the taxa that have been forgotten and completely excluded from the European fauna is *Glomeris herzogowinensis* Verhoeff, 1898. Verhoeff (1898) described this taxon under the name "*Glomeris europaea*, *herzogowinensis*" on the basis of specimens from near Trebinje, Herzegovina, collected by Victor Apfelbeck, the then curator of the National Museum of Bosnia and Herzegovina in Sarajevo. Although the description of this taxon is relatively short, Verhoeff (1898) already points out in the first sentence: "...der marginata in der Färbung äusserst ähnlich...", indicating a great similarity in colouration between *G. herzogowinensis* and one of the most common western-central-northern European species, *Glomeris marginata* (Villers, 1789). Albeit geographically completely separate, both species are characterised by mostly black, shiny tergites with yellowish or white posterior margins. Verhoeff (1898) noted several differences between the two taxa, including details of the telopods, although he never illustrated them. This deficiency led to *G. herzogowinensis* falling into oblivion. Two years later, Verhoeff (1901: 248, 249) cited *G. herzogowinensis* from several localities in Albania and Greece, apparently only on the basis of a large, dark body with lighter posterior margins, evidently without examining the telopods of males from Greece. Later, it will turn out that, in these parts of Albania and Greece, there is or are one or even two species similar in appearance to *G. herzogowinensis*, but belonging to a different genus, *Onychoglomeris* Verhoeff, 1906. The fact that Verhoeff did not actually examine the telopods of the Greek male specimens is supported by the fact that, when establishing the then subgenus, *Onychoglomeris*, he included in it what we know today as *Onychoglomeris tyrolensis* (Latzel, 1884) and *Simplomeris montivaga* (Faës, 1902) (Verhoeff 1906). The telopods of these species differ markedly from those of the genus *Glomeris* and *G. herzogowinensis*. In his contribution to the knowledge of the genus *Glomeris*, Verhoeff (1911: 118, 119) included *Glomeris herzogowinensis* in the *marginata* species-group, stating some of the characteristics of the species. It is clear from the above that the species he described from the Trebinje area really belongs to the genus *Glomeris*.

However, the problem emerged in the papers of Attems (1929, 1935), after which the species name *Glomeris herzogowinensis* was no longer mentioned. Strangely and without any explanation, Attems (1929: 289, 312) listed Verhoeff's species under the name "*Onychoglomeris herzegovinensis* Verh.". The crux of the problem with this taxon happened six years later. Probably confused by Verhoeff's (1901: 248, 249) earlier (obviously incorrect) record of *G. herzogowinensis* from Albania and Greece and the confusing similarity in the habitus between the latter species of which he received some syntypes and the specimens of the genus *Onychoglomeris* from Albania and Greece he was studying, Attems (1935) just treated the species *G. herzogowinensis* as *Onychoglomeris herzogowinensis*. Attems (1935) was not sure of his act, especially because the structure of the telopods of *G. herzogowinensis* was unknown to him. He stated that only Verhoeff could clarify this by examining the telopods, although Attems himself could have done so (see below in Remarks under *G. herzogowinensis*). Despite this error, Attems was, however, right in the fact that his new specimens belonged to the genus *Onychoglomeris*. He described two taxa: *Onychoglomeris herzegovinensis media* Attems, 1935 from Albania and *O. h. australis* Attems, 1935 from Greece (Attems 1935). He treated the taxon from Croatia, Bosnia and Heregovina and Montenegro as the nominotypical subspecies *O. h. herzegovinensis* (*herzogowinensis* is the correct spelling in all cases). Attems (1935) provided illustrations of the telopods of the two subspecies, which undoubtedly speak in favour of the genus *Onychoglomeris*, but at the same time, he pointed out some differences in habitus between his subspecies on the one hand and the nominotypical subspecies distributed further north on the other.

Six decades later, Mauriès et al. (1997), based on relatively abundant material of *Onychoglomeris* from Albania, but without studying the specimens from the type locality of *G. herzogowinensis* nor the Greek specimens of *Onychoglomeris*, questioned the existence of three subspecies, considered all under the name *Onychoglomeris herzogowinensis*. The name appeared as such in Thaler (1999) and Kime and Enghoff (2011).

Based on newly-collected material from near the type localities and on the study of the syntypes and historical specimens of Verhoeff's *G. herzogowinensis* and Attems' subspecies *O. h. australis* and *O. h. media*, we revive Verhoeff's species *Glomeris herzogowinensis* after almost nine decades and we consider both of Attems' subspecies as species, viz. *Onychoglomeris australis* Attems, 1935 stat. nov. and *Onychoglomeris media* Attems, 1935 stat. nov.

## Materials and methods

Live specimens were collected by hand and preserved in 70% ethanol for mophological and 96% ethanol for DNA analyses. Several live individuals of *Glomeris herzogowinensis* were first placed in glass vials containing 500 µl methylene chloride (DCM) for 5 minutes to extract their defensive secretions for future semiochemical studies. Later, the specimens were transferred to 70% ethanol.

## Depository

**IZB** Institute of Zoology, University of Belgrade – Faculty of Biology, Belgrade, Serbia
**NHMW** Naturhistorisches Museum Wien, Vienna, Austria
**ZFMK** Zoological Research Museum A. Koenig, Leibniz Institute for Biodiversity Change, Bonn, Germany
**ZMB** Museum für Naturkunde Berlin, Germany
**ZSM** Zoologische Staatssammlung München, Germany

## Morphology, photography and map

Specimens were examined with a Nikon SMZ 25 (NHMW), Nikon SMZ 745T, Nikon SMZ 1270 (IZB) or Olympus SZX12 (ZFMK) binocular stereomicroscopes. Old microscopic preparations were examined with a Nikon SMZ 25 (NHMW) binocular stereomicroscope or with a Carl Zeiss Axioscope 40 microscope (IZB). Photographs of habitus, leg pairs 17 and 18 and telopods were taken using a Nikon DS-Ri-2 camera mounted on a Nikon SMZ25 binocular stereomicroscope using NIS-Elements Microscope Imaging Software with an Extended Depth of Focus (EDF) patch (NHMW, Figs 2–6, 8–11A–D, G) or with a Nikon DS-Fi2 camera with a Nikon DS-L3 camera controller attached to a Nikon SMZ 1270 binocular stereomicroscope (IZB, Fig. 11E, F). The photos of the living animals were taken with a Canon PowerShot SX530 HS (Fig. 7A, B), Olympus Stylus Tough TG-6 (Fig. 7C, D), Nikon D750 (Fig. 12A, B) and Panasonic DMC-G81 (Fig. 12E, F) digital cameras as well as with a cellphone (Fig. 12C, D). The distribution map was created using Google Earth Pro (version 7.3.6.9750) and Adobe Photoshop CS6. The final images were processed and assembled in Adobe Photoshop CS6.

## DNA extraction, amplification and sequencing

In order to find close relatives to *Glomeris herzogowinensis*, as well as *Onychoglomeris australis* stat. nov., a DNA barcoding analysis (Hebert et al. 2003) was conducted. COI sequences of both taxa, as well as those of potential related *Glomeris* species, such as *G. balcanica* Verhoeff, 1906 and *G. pulchra* Koch, 1847 and additionally *Onychoglomeris ferraniensis* Verhoeff, 1909 were analysed (see Table 1). In addition, sequences of similarily coloured (= black) *Glomeris* species were downloaded from GenBank: *Glomeris marginata* (Villers, 1789) from Central Europe, *G. apuana* Verhoeff, 1911 from the Apuan Alps and *G. maerens* Attems, 1927 from Spain. Additionally, sequences of widespread species occurring in the Balkans and surrounding areas were added from GenBank: *G. pustulata* Latreille, 1804, *G. hexasticha* Brandt, 1833, *G. tetrasticha* Brandt, 1833 and *G. klugii* Brandt, 1833. As outgroup taxa, sequences of *Glomeridella minima* (Latzel, 1884) and *Tonkinomeris huzhengkuni* Liu & Golovatch, 2020 from the family Glomeridellidae Cook, 1896 were added. Our dataset included 25 COI sequences from 15 species, of which eight sequences from five species were newly sequenced.

The DNA extraction, amplification and sequencing protocol was similar to earlier studies (Wesener 2015a; Sagorny and Wesener 2017), using the degenerate (Astrin and Stüben 2008) primer pair HCO-JJ/LCO-JJ (HCOJJ AWACTTCVGGRTGVCCAAARAATCA/ LCOJJ CHACWAAYCATAAAGATATYGG). Sequences were concatenated by hand or by utilising the software Seqman (DNASTAR Inc.). BLAST searches (Altschul et al. 1997) were performed to confirm sequence identities. The whole dataset was translated into amino acids to rule out the accidental amplification of pseudogenes. The eight new sequences have been uploaded to GenBank under the accession codes PP475126–PP475133 (Table 1). All sequences were aligned in Bioedit (Hall 1999).

The number of base differences per site (p-distances) between sequences was calculated (See Suppl. material 1). The analysis involved 25 nucleotide sequences. Codon positions included were $1^{st}+2^{nd}+3^{rd}$. All ambiguous positions were removed for each sequence pair. There were a total of 657 positions in the final dataset. Evolutionary analyses were conducted in Mega11 (Tamura et al. 2021).

The best fitting substitution model for a Maximum Likelihood analysis was calculated with ModelTest (Tamura and Nei 1993) as implemented in MEGA11. The best fitting model was the general time reversible (GTR)-Model (Tavaré 1986) with gamma distribution and invariant sites (GTR+G+I) (lnL = -4292.222, Invariant = 0.609, Gamma = 0.624, Freq A: 25.7, T: 38.89, C: 14.17, G: 21.24).

The evolutionary history was inferred by using the Maximum Likelihood method and the General Time Reversible model (GTR+G+I) (Nei and Kumar 2000). The tree with the highest log likelihood (-4292.19) is shown in Fig. 1. Initial trees for heuristic search were automatically obtained by applying Neighbour-Joining and BioNJ algorithms to a matrix of pairwise distances estimated using the Maximum Composite Likelihood (MCL) approach. Codon positions included were $1^{st}$-$2^{nd}$-$3^{rd}$. All positions with less than 95% site coverage were eliminated, i.e. fewer than 5% alignment gaps, missing data and ambiguous bases were allowed at any position (partial deletion option). There were a total of 657 positions in the final dataset. The bootstrap consensus tree was calculated from 1000 replicates (Felsenstein 1985) in MEGA11 (Tamura et al. 2021). The obtained tree was edited in Adobe Illustrator 2023 with all bootstrap values > 50% illustrated (Fig. 1).

**Table 1.** Newly-analysed specimens, vouchers and GenBank numbers. More detailed localities are only given for newly-sequenced specimens. Abbreviations: **SCAU** = South China Agricultural University, Guangzhou, China; **ZSM** = Bavarian State Collection, Munich, Germany; **ZFMK** = Zoological Research Museum Koenig, Leibniz Institute for the Analysis of Biodiversity Change (LIB), Bonn, Germany.

| Species | Locality | Voucher # | GenBank # |
|---|---|---|---|
| *Glomeridella minima* (Latzel, 1884) | Austria | ZSM MYR 00371 | JN271878 |
| *Tonkinomeris huzhengkuni* Liu & Golovatch, 2020 | China | SCAU TY01 | MT522013 |
| *Glomeris pustulata* Latreille, 1804 | Germany | ZSM MYR 00024 | HM888093 |
| *Glomeris pustulata* Latreille, 1804 | Germany | ZSM MYR 00376 | JN271880 |
| *Glomeris hexasticha* Brandt, 1833 | Germany | ZFMK MYR1460 | MG931023 |
| *Glomeris hexasticha* Brandt, 1833 | Germany | ZFMK MYR3898 | MG931024 |
| *Glomeris tetrasticha* Brandt, 1833 | Germany | ZSM MYR 00036 | HM888105 |
| *Glomeris tetrasticha* Brandt, 1833 | Germany | ZSM MYR 00035 | HM888104 |
| *Glomeris marginata* Villers, 1789 | France | ZFMK MYR6084 | MG931022 |
| *Glomeris marginata* Villers, 1789 | Luxembourg | ZFMK MYR1363 | MG931021 |
| *Glomeris maerens* Attems, 1927 | Spain | ZFMK MYR6097 | MG892108 |
| *Glomeris maerens* Attems, 1927 | Spain | ZFMK MYR6092 | MG892110 |
| *Glomeris klugii* Brandt, 1833 | Italy | ZFMK MYR637 | KX714076 |
| *Glomeris klugii* Brandt, 1833 | Italy | ZFMK MYR4734 | KX714072 |
| *Glomeris apuana* Verhoeff, 1911 | Italy | ZFMK MYR753 | KT188944 |
| *Glomeris apuana* Verhoeff, 1911 | Italy | ZFMK MYR752 | KT188943 |
| *Onychoglomeris tyrolensis* Latzel, 1884 | Italy | ZFMK MYR1276 | KP205571 |
| *Glomeris pulchra* Koch, 1847 | Croatia, Dalmatia, Cetina River | ZFMK MYR8217 | PP475126 |
| *Glomeris pulchra* Koch, 1847 | Croatia, Dalmatia, Cetina River | ZFMK MYR8217b | PP475127 |
| *Glomeris balcanica* Verhoeff, 1906 | Greece, Dion-Olympos | ZFMK MYR11331 | PP475128 |
| *Onychoglomeris ferraniensis* Verhoeff, 1909 | Italy, Piemonte, Cuneo, Ceva | ZFMK MYR623 | PP475129 |
| *Onychoglomeris ferraniensis* Verhoeff, 1909 | Italy, Piemonte, Cuneo, Ormea | ZFMK MYR2287 | PP475130 |
| *Onychoglomeris australis* Attems, 1935 stat. nov. | Greece, Kalambaka | ZFMK MYR11332 | PP475131 |
| *Glomeris herzogowinensis* Verhoeff, 1898 | Bosnia & Herzegovina, Trebinje, Taleža | ZFMK MYR8970 | PP475132 |
| *Glomeris herzogowinensis* Verhoeff, 1898 | Bosnia & Herzegovina, Trebinje, Taleža | ZFMK MYR8969 | PP475133 |

# Results

## Analysis of the COI barcoding gene

All species were recovered with high statistical support (94–100%, Fig. 1), while deeper nodes and interspecific relationships were statistically not supported. Neither the families Glomeridae and Glomeridellidae, nor the genus *Glomeris* are recovered as monophyletic (Fig. 1). *Glomeris herzogowinensis* does not group with *Onychoglomeris* species, but is in an unsupported sister-group with the similarily coloured *G. maerens* from the Mediterranean coast of Spain (Fig. 1). *G. herzogowinensis* and *G. maerens* show also the lowest genetic distance to one another (11.9–12.6%), while *G. herzogowinensis* also shows lower genetic distances to the similarily coloured (black) *G. apuana* (12.2–12.9%) and the Balkan *G. balcanica* (12.6–13.4%), while it shows genetic distances of 13.4–16.4% to all other analysed species. The genus *Onychoglomeris* is recovered as monophyletic with moderate statistical support (74), with *O. australis* stat. nov. and the Italian *O. tyrolensis* in a weakly-supported sister-group (54, Fig. 1). *O. australis* stat. nov. shows the lowest genetic distance to *O. tyrolensis* (10.5%) and *O. ferraniensis* (11.1–11.4%), while it differs from species of the other genera by 12.8–15.7%.

## Taxonomy

**Class Diplopoda de Blainville in Gervais, 1844**
**Order Glomerida Brandt, 1833**
**Family Glomeridae Leach, 1816**
**Subfamily Glomerinae Leach, 1816**
**Genus *Glomeris* Latreille, 1802**

### *Glomeris herzogowinensis* Verhoeff, 1898

Figs 1–7

*Glomeris europaea, herzogowinensis* Verhoeff, 1898: 163, fig. 18.
not *Glomeris herzegowinensis* (sic!).– Verhoeff (1901: 248).
not *Glomeris herzegowinensis*.– Verhoeff (1901: 249).
*Gl. herzegowinensis* (sic!).– Verhoeff (1906: 211).
*herzegowinensis* (sic!).– Verhoeff (1911: 119). [in the genus *Glomeris*].
*Onychoglomeris hercegovinensis* (sic!) in part.– Attems (1929: 289, 312).
*Onychoglomeris hercegovinensis hercegovinensis* (sic!).– Attems (1935: 149).
*Onychoglomeris hercegovinensis hercegovinensis* (sic!).– Attems (1959: 323).
*Onychoglomeris herzegowinensis* (sic!).– Strasser (1971: 12).
not *Onychoglomeris herzegowinensis* (sic!).– Thaler (1999: 198, 199, figs 16, 17).
*Glomeris marginata*.– Ceuca (1990: 10).
*Onychoglomeris herzogowinensis* in part.– Kime and Enghoff (2011: 34, 118).

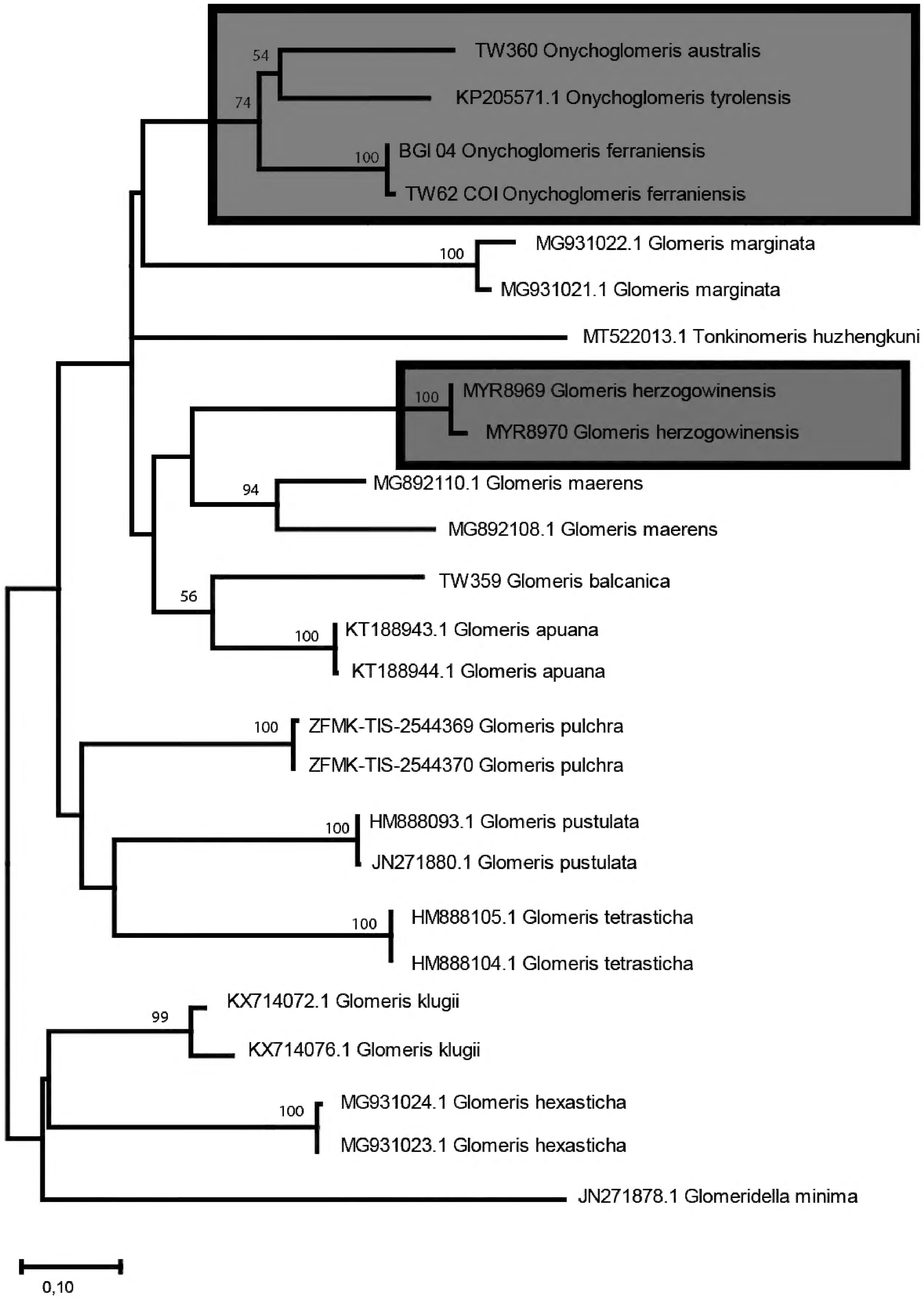


**Figure 1.** Maximum Likelihood tree (ML) of millipedes of the order Glomerida, based on 657 bp of the COI gene. Yellow box = *Onychoglomeris* Verhoeff, 1906; blue box = *Glomeris herzogowinensis* Verhoeff, 1898. Numbers on nodes are bootstrap values from the ML analysis and are shown when > 50%.

**Diagnosis.** Large species (up to 20 mm) with mostly black, shiny tergites with contrasting yellowish or white posterior margins. Similar to *G. marginata* in general appearance, but differs by strongly-pronounced light-coloured anterolateral margins of the thoracic shield which is in the form of a narrow band in *G. marginata*. Additionally, *G. herzogowinensis* has two complete or almost complete striae on the thoracic shield (tergite 2), while *G. marginata* has one complete stria.

**Material studied.** ***Lectotype.*** 1 male (NHMW 3903); Bosnia and Herzegovina, Trebinje; V. Apfelbeck leg.; K. Verhoeff don. 1897. Lectotype here designated.

***Paralectotypes.*** ● 1 male, slide preparation (ZMB-MYR12772) (Verhoeff slide 953): leg pair 18 and telopods; Trebinje. ● 1 male, 1 female (ZMB-MYR2261); Trebinje.

***?Types***. ● 1 female (NHMW MY10415); Herzegovina: K. Verhoeff don. 1899. (Although this female arrived later in the NHMW collection than the lectotype, it may well represent another type specimen collected by Apfelbeck near Trebinje). ● 2 tubes (ZSM-A 20070848), 1 whole male, 1 male dissected (missing telopods and posterior leg pairs), 1 female, 1 juvenile; "ehemals Trockenmaterial" [material previously dry], Etk Nb. 28; Herzegowina. ● 1 tube (ZSM-A20070848), (Etk Nb. 28): 1 entire female specimen, a detached collum and thoracic shield, "ehemals Trockenmaterial; Tier m Original determinat. Etikett C Typüs-verdächtig" [material previously dry, animal with original determination, probable type], Trebinje. ● 1 male, slide preparation (ZSM-A20031802): telopods, leg pairs ?16, 17 and 18; Schuma (= Šuma, karst region around Trebinje).

**Other material examined.** Bosnia and Herzegovina: ● 1 female (NHMW MY10414); Trebinje ● 2 males, 1 female (IZB); in front of Taleža Cave, Taleža Village, near Trebinje, under stones; 15 November 2019; D. Antić leg. ● 3 males, 7 females (IZB); same locality as previous; 8 April 2022; D. Antić and D. Stojanović leg. ● 1 female (IZB); in front of Pavlova Cave, Bihovo Village, near Trebinje, under a stone; 16 November 2019; D. Antić leg. ● 1 female (IZB); same as previous but inside Pavlova Cave. Croatia: ● 1 female (NHMW MY10427); Pridvorje ● 2 females (ZFMK MYR89); Dubrovnik-Neretva, Konavle Region, Gruda, Konavoski dvori, under stones close to river, 50 m elev.; 3 April 2010; R. Ozimec & A. Schönhofer leg. ● 1 male (ZFMK MYR95); Dubrovnik-Neretva, Konavle Region, Vignje, near Sklenica Cave, under stones in dense, humid, mossy forest, 89 m elev.; 3 April 2010; R. Ozimec & A. Schönhofer leg. ● 3 males (ZFMK MYR153); Dubrovnik-Neretva, Konavle region, Vignje, Špilja at Vignje Cave; under stones; 3 April 2010; R. Ozimec & A. Schönhofer leg. ● 1 female (ZFMK MYR173); Dubrovnik-Neretva, Konavle Region, Vignje, surroundings of entrance of Tunnel of Konavle Polje, under stones, 50 m elev.; 3 April 2010; R. Ozimec & A. Schönhofer leg. Montenegro: ● 1 male, 4 females (NHMW MY10413); Savina ● 1 male (IZB) ethanol and slide with leg pairs 17 and 18 and telopods; Orjen Mountain, Balješina Lokva, 1400 m elev.; 4 July 1997; I. Karaman leg. ● 1 female (ZFMK MYR220); Rumija Mountain, near Sutorman, sieving in oak forest near rocks and under stones along open path, 42°9'22.8"N, 19°6'32.1"E, 805 m elev.; 9 May 2006; A. Schönhofer leg. ● 1 ex.; Borovik, near Cetinje; 11 May 2011; D. Antić observed.

**Remarks.** After examining type and old museum specimens, as well as freshly-collected animals, we confidently conclude that Verhoeff's *herzogowinensis* has typical *Glomeris* telopods. Attems (1935) examined

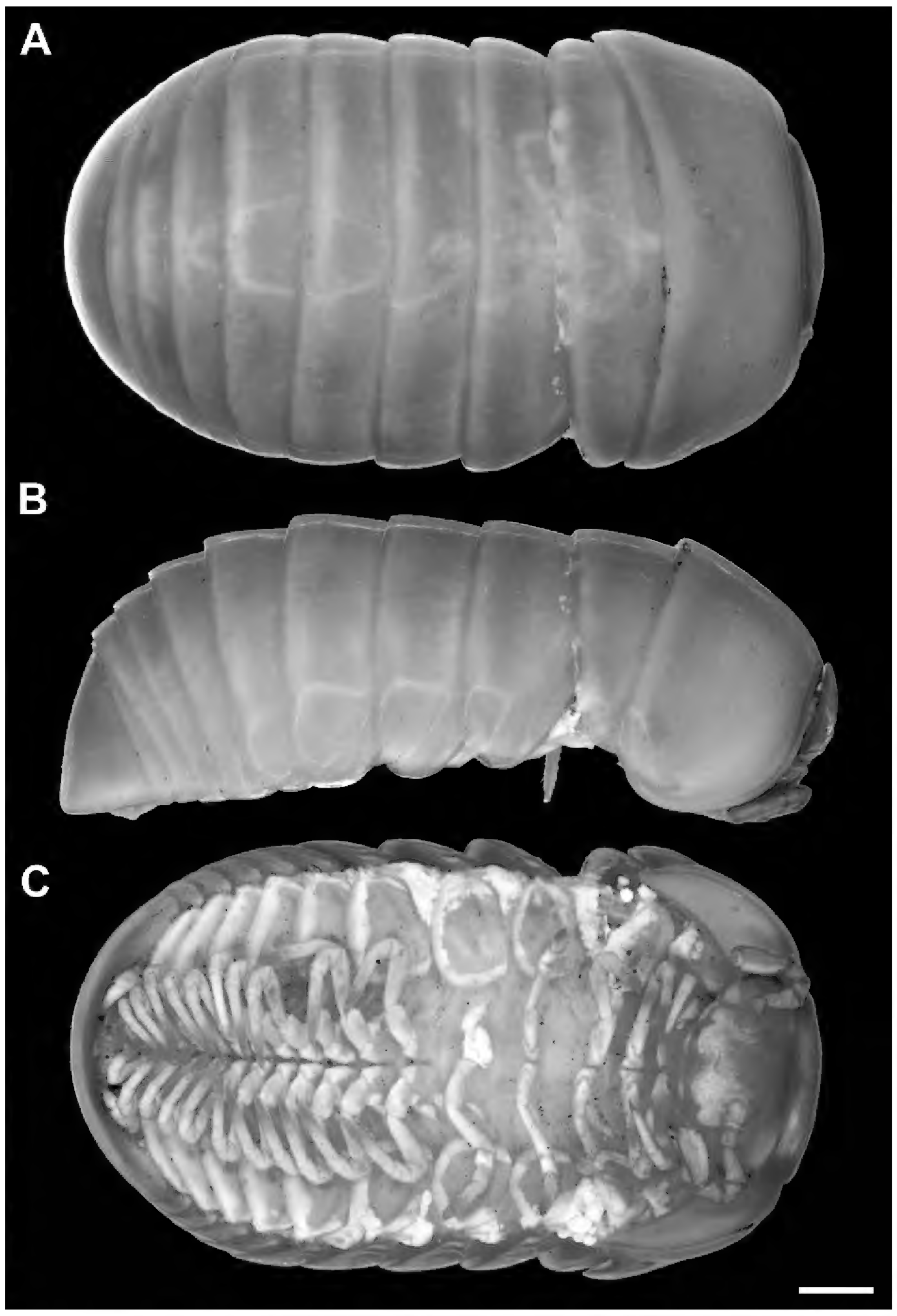


**Figure 2.** *Glomeris herzogowinensis* Verhoeff, 1898, lectotype male (NHMW MY3903), habitus. **A.** Dorsal view; **B.** Lateral view; **C.** Ventral view. Scale bar: 1 mm.

Verhoeff's material sent to the NHMW and listed that they were both females, so there was no possibility of examining the telopods. Interestingly, we found and examined these two specimens, among which one revealed to actually be a male (now lectotype, see Figs 2, 3). In addition, Attems (1929) indicated the locality Savina in Montenegro as one of the collecting cites of *Onychoglomeris hercegovinensis* (sic!). We found one male (Fig. 4) among five specimens from this locality, again with typical *Glomeris* telopods (Fig. 4D). Thus, Attems missed the opportunity to see the telopods in two males, including Verhoeff's syntype and to conclude that it was, indeed, a species of the genus *Glomeris* and not of *Onychoglomeris*.

*Glomeris herzogowinensis* shows a striking resemblance with *G. marginata*, both in habitus (Figs 5–7) and in the structure of the telopods (Figs 3C, 4D), which are almost identical in both species. Verhoeff (1898) pointed out that *G. herzogowinensis* has more prominent light-coloured posterolateral margins compared to *G. marginata*. However, this is not entirely correct, as one individual analysed by us (Fig. 6A) has identical margins to most *G. marginata*. Indeed, most of the studied specimens of *G. herzogowinensis* have more pronounced margins than the classic *G. marginata*, but

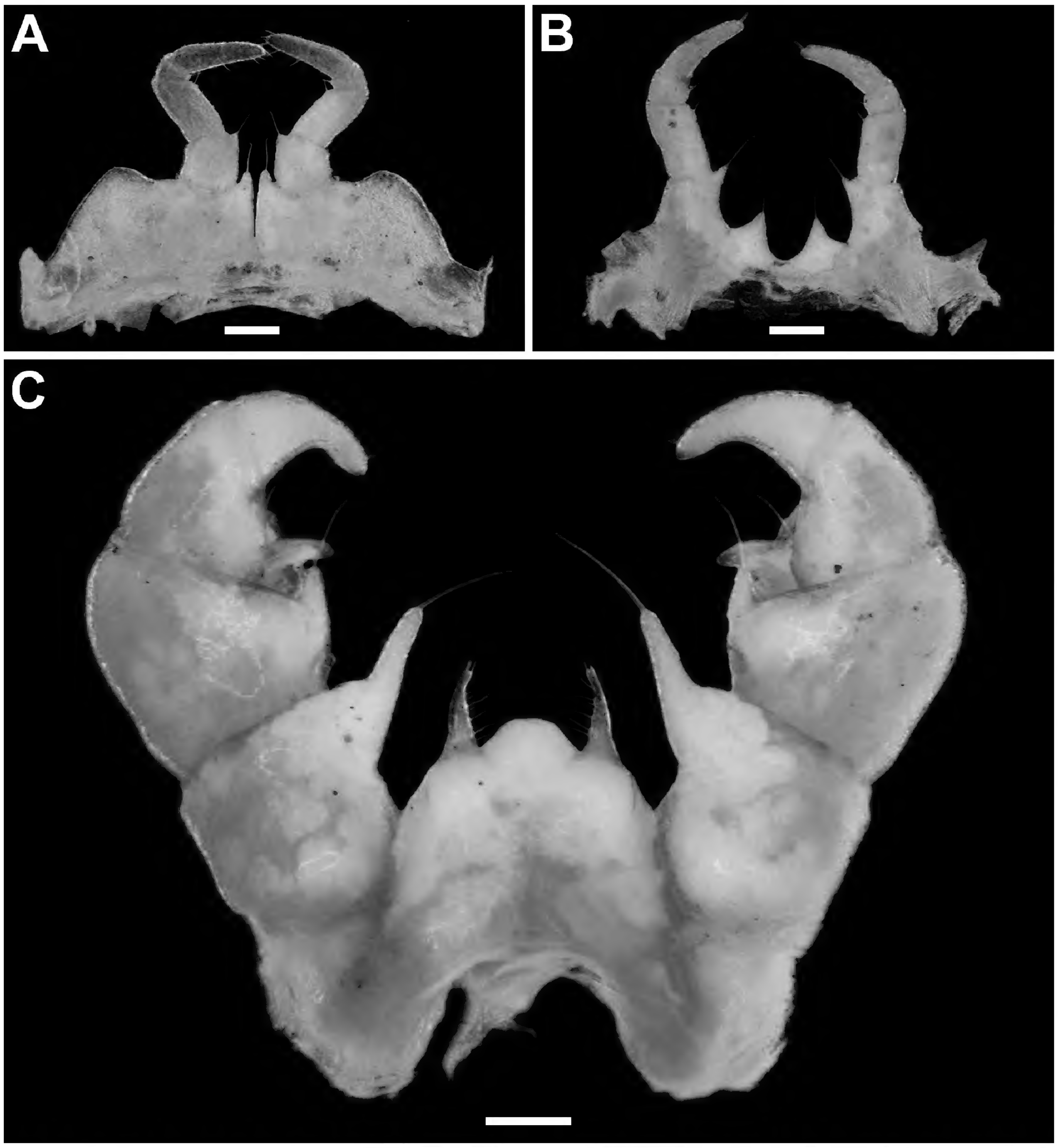


**Figure 3.** *Glomeris herzogowinensis* Verhoeff, 1898, lectotype male (NHMW MY3903). **A.** Leg pair 17, anterior view; **B.** Leg pair 18, anterior view; **C.** Telopods, anterior view. Scale bars: 0.2 mm.

some French populations of the latter present posterolateral margins that are more developed than in *G. herzogowinensis* (see Reip and Wesener (2018: 96, fig. 1D, E)). Verhoeff (1898, 1911) mentioned the presence of strongly-pronounced light-coloured anterolateral margins of the thoracic shield as one of the most important features distinguishing these two species. Indeed, the thoracic shield of all examined individuals of *G. herzogowinensis* has very distinct anterolateral margins (Figs 5A, C, 6B, D, E), in contrast to *G. marginata*, where it is only present in the form of a narrow band. The colouration of the fresh specimens that we have analysed corresponds completely to the description of Verhoeff (1898). They are mostly black with clearly demarcated lighter, whitish or yellowish posterolateral margins of the tergites. The collum also has a lighter posterior margin, as does the anal shield. As already mentioned, the thoracic shield also has a pronounced anterolateral margin. Some specimens are characterised by the presence of a pair of pale marbled patches on the tergites, including the thoracic shield, as well as an unpaired patch on the anal shield (Figs 5A, B, D, 6B). The presence of demarcated posterolateral light-coloured margins is clearly visible in old museum specimens too (Figs 2A, B, 4A).

Verhoeff (1898) listed some differences in the structure of the telopods, but they were apparently so insignificant that he never drew these structures. Nevertheless, in this paper, we present for the first time illustrations of the telopods of *G. herzogowinensis*, as well as of the 17$^{th}$ pair of legs and the entire 18$^{th}$ pair of legs (Figs 3, 4B–D), which are of typical *Glomeris* appearance.

We would also like to mention that all examined specimens show two transverse ridges on the collum (Figs 5C, 6B, E). Verhoeff (1911) found that, in addition to the two characteristic ridges, a third ridge starts on both sides of the collum. In the fresh material, the beginning of the third ridge was only observed in one specimen and only on the left side. Concerning the thoracic shield (tergite 2), Verhoeff (1898) distinguished *G. herzogowinensis* from *G. marginata* by the presence of two complete striae and an incomplete one (2+1 vs. 1+2, 1+1 or 1+0 sensu Schubart (1934: 33, fig. 28)). Indeed, all but

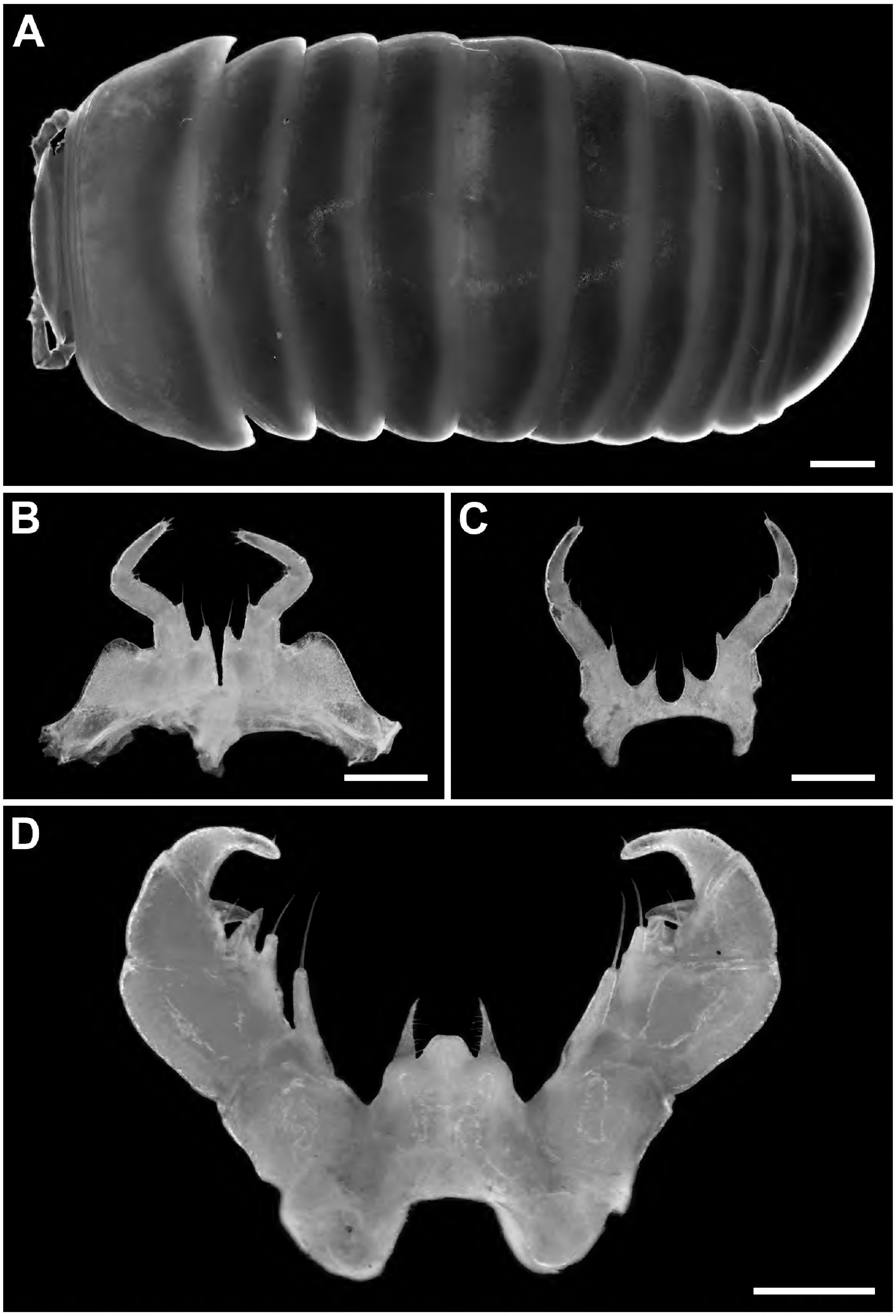


**Figure 4.** *Glomeris herzogowinensis* Verhoeff, 1898, male from Savina, Montenegro (NHMW MY10413). **A.** Habitus, dorsal view; **B.** Leg pair 17, anterior view; **C.** Leg pair 18, anterior view; **D.** Telopods, anterior view. Scale bars: 1 mm (**A**); 0.5 mm (**B–D**).

two of the specimens examined show two complete striae and an incomplete one. In two specimens, the second stria is almost complete, with only a small interruption dorsally. Some specimens are characterised by the presence of additional, 4th incomplete striae in front of the first complete one.

**Habitat.** Known from almost near sea level up to 1400 m elev. in the Orjen Mountain. Scrubs of *Carpinus*, *Quercus*, *Juniperus*, under stones in limestone areas. Inside caves.

**Distribution.** The extreme south of Croatia and Bosnia and Herzegovina, as well as the coastal part of

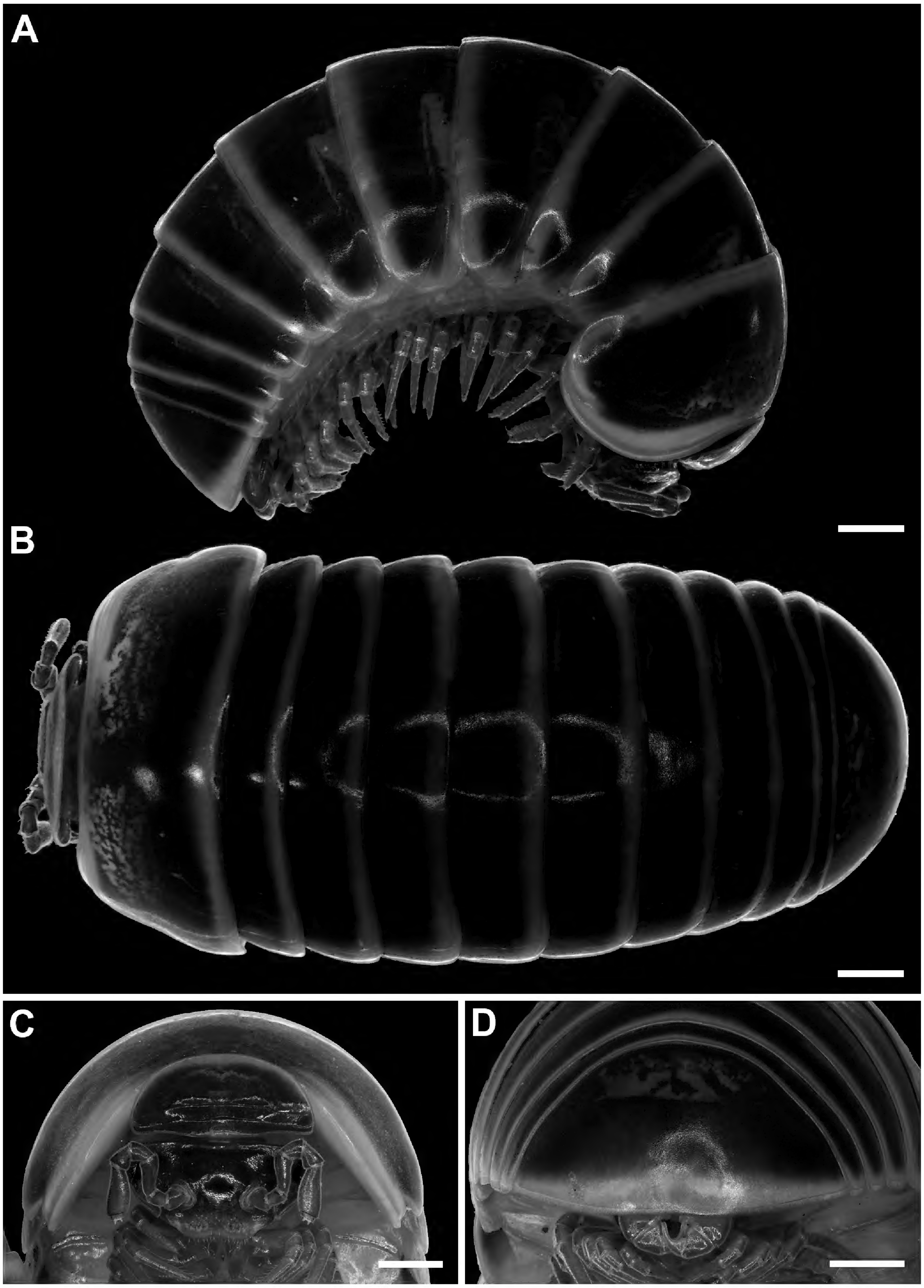


**Figure 5.** *Glomeris herzogowinensis* Verhoeff, 1898, male from Taleža, Bosnia and Herzegovina (IZB). **A.** Habitus, lateral view; **B.** Habitus, dorsal view; **C.** Head, collum and thoracic shield, anterior view; **D.** Anal shield, posterior view. Scale bars: 1 mm.

Montenegro (Fig. 13). Endemic south Dinaric coastal species. Croatia: Pridvorje (Attems 1929), Konavoski Dvori (Ceuca 1990, as *G. marginata*; present study), Gruda near Konavle (T. Dražina pers. comm.; present study), Vignje (present study); Bosnia and Herzegovina: Surroundings of Trebinje (Verhoeff 1898; Attems 1929, 1935), Taleža near Trebinje (present study), Bihovo near Trebinje (present study). Montenegro: Savina (Attems 1929, 1935), Orjen (present study), Rumija, near Sutorman (present study), Cetinje, Borovik (present study).

**Type locality.** Near Trebinje, Bosnia and Herzegovina.

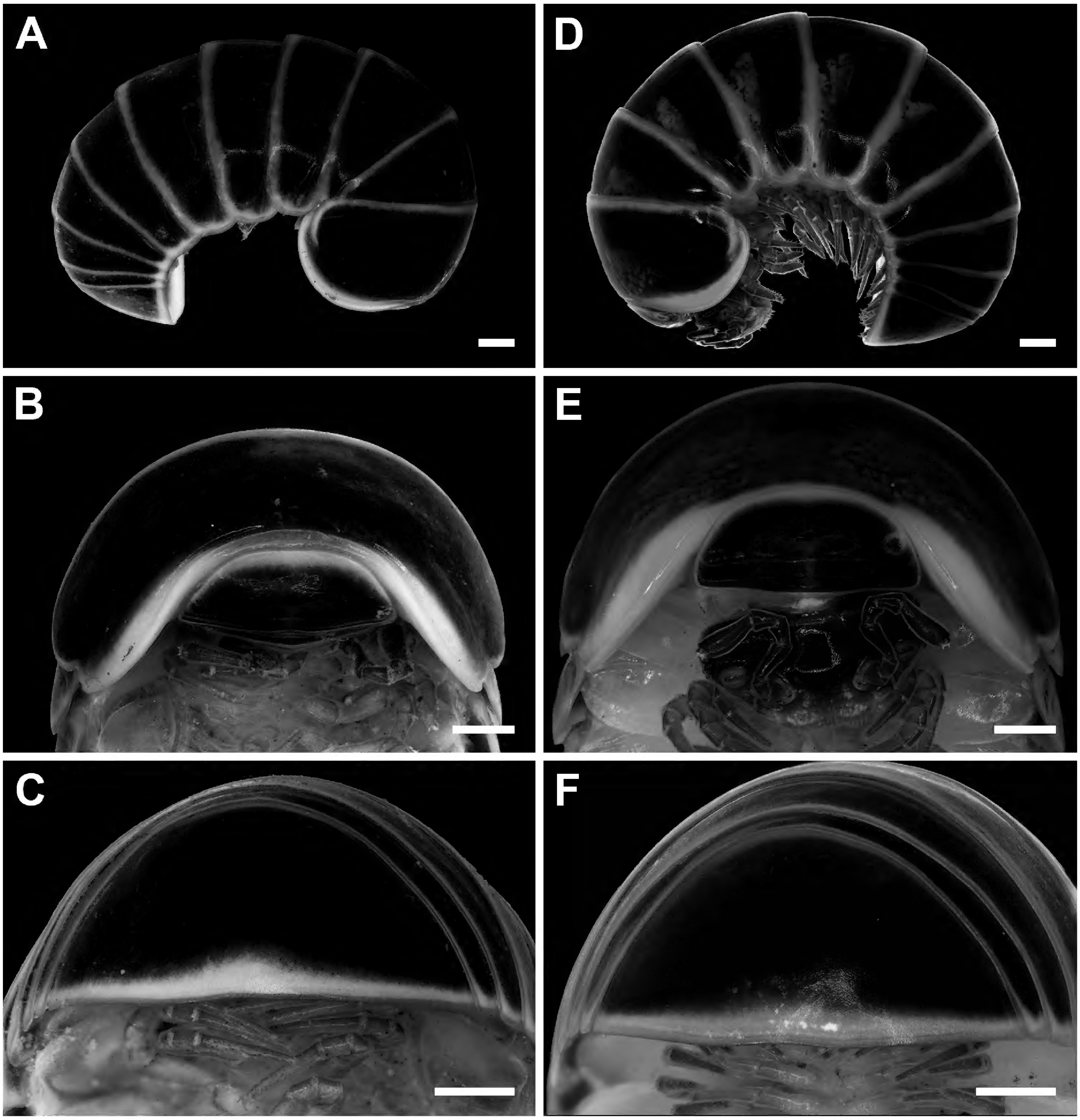


**Figure 6.** *Glomeris herzogowinensis* Verhoeff, 1898, male (**A–C**) and female (**D–F**) from Taleža, Bosnia and Herzegovina (IZB). **A.** Habitus, lateral view; **B.** Collum and thoracic shield, anterior view; **C.** Anal shield, posterior view; **D.** Habitus, lateral view; **E.** Head, collum and thoracic shield, anterior view; **F.** Anal shield, posterior view. Scale bars: 1 mm.

## Genus *Onychoglomeris* Verhoeff, 1906

### *Onychoglomeris australis* Attems, 1935, stat. nov.

Figs 8, 9, 12A–D

*Onychoglomeris hercegovinensis australis* (sic!).– Attems (1935: 150, figs 6–8).

*Glomeris herzogowinensis* in part.– Verhoeff (1901: 249).

*Onychoglomeris herzegowinensis australis* (sic!).– Strasser (1976: 580).

*Onychoglomeris herzegowinensis* (sic!).– Thaler (1999: 198, 199, figs 16, 17).

*Onychoglomeris herzogowinensis* in part.– Kime and Enghoff (2011: 34, 118).

**Diagnosis.** Similar in colouration (Fig. 12A–D) and morphology to the geographically very close *O. media* stat. nov., but differs in the appearance of the anal shield, leg pair 18 and telopods. Anal shield straight in lateral view (vs. distinctly concave in *O. media* stat. nov.). Leg pair 18 with short podomere 2, which is 1.5 times longer than wide, with straight mesal margin (vs. podomere 2 longer, twice as long as wide with distinctly convex mesal margin in *O. media* stat. nov.). Telopods apparently less robust, with a less developed posteriomesal process of telopoditomere 2 (= femur) and a shorter telopoditomere 4 (= tarsus), brownish stripes at the base of posteromesal process of telopoditomere 2 absent (vs. present in *O. media*

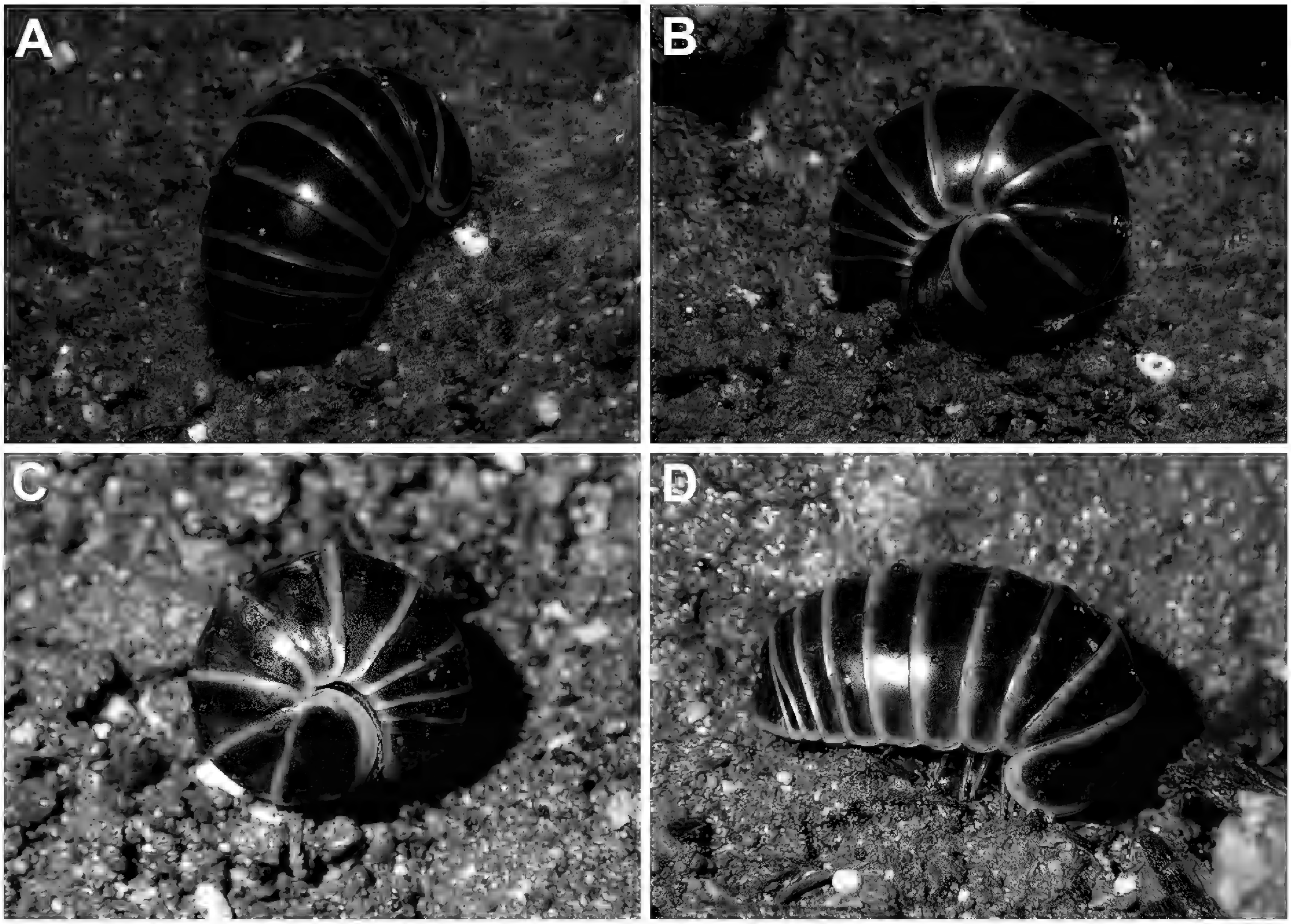

**Figure 7.** *Glomeris herzogowinensis* Verhoeff, 1898, living specimens. **A, B.** Female from Pavlova Cave, Bosnia and Herzegovina (IZB); **C, D.** Specimen from Taleža, Bosnia and Herzegovina (IZB). Photos by Dragan Antić.

stat. nov.), telopoditomere 3 (= tibia) with a well-developed posterior tooth that is more or less conical (vs. tooth poorly developed, subtriangular, sometimes almost absent in *O. media* stat. nov.), the syncoxite is usually high, rounded (vs. syncoxite mostly lower, bilobed in *O. media* stat. nov.). For more details see remarks below.

**Material studied.** ***Lectotype.*** 1 male (NHMW MY10424); Greece, Epirus, Athamanika (= Tzoumerka) Mountain, Paraskevi, *Abies*, 1400 m elev.; 16 June 1933; M. Beier leg. Lectotype here designated.

***Paralectotypes.*** 13 males, 11 females (NHMW MY3900); same data as for lectotype. Including one slide (NHMW MY3900) with two pairs of leg pair 18, two pairs of leg pair 17 and additional leg ?17.

**Other material examined.** All in Greece: ● 1 male (NHMW MY10418); Epirus, Buka Chalasmata near Platanoussa; 14 May 1932; M. Beier leg. ● 2 males, 2 females (NHMW MY10419); Epirus, Katarraktis; 1932/1933; M. Beier leg. ● 1 female (NHMW MY10416); Prosgoli; V. Apfelbeck leg. ● 5 males (NHMW MY10420); Epirus, Aoos Gorge near Konitsa, 550 m elev., *Carpinus*; 9 September 1996; K. Thaler and B. Knoflach leg. ● 8 males, 5 females (NHMW MY10421); Epirus, Timfi Mountain near Micropapingo, 800 m elev., bush; 10 September 1996; K. Thaler and B. Knoflach leg. ● 1 female (ZFMK MYR122); Epirus, Pindus Mountain, Zagori, Monodendri - Ano Pedina junction, under stone on the road, 835 m elev., 39.868002, 20.722076; 3 April 2006; A. Schönhofer leg. ● 5 males, 5 females, 2 juveniles (ZFMK MYR4517); Epirus, Vikos Gorge, near Monodendri, *Quercus* forest with lichens, 1000 m elev., 39.881527, 20.755473; 4 April 2006; A. Schönhofer leg. ● 7 males, 2 females, (ZFMK MYR4518); Epirus, SW Ioannina, Zoodochos Pigi, open bushland with partly evergreen *Quercus* close to stream under stones, old tree trunks and sieving from leaf litter, 460 m elev., 39.56492, 20.72300; 13 August 2009; S. Huber & A. Schönhofer leg. ● 1 female (ZFMK MYR162); Thessaly, road to Kastanea, Elafi, *Carpinus*, *Quercus*, N-exposition, sieving from depressions in trees, 454 m elev., 39.723250, 21.475917; 1 April 2006; A. Schönhofer leg. ● 2 males, 4 females (ZFMK MYR124); Thessaly, road E92a between Panagia and Metsovo; sieving in a damp, shady stream valley, moss and between stones, pine forest and alpine meadows, 1084 m elev., 39.80344, 21.306998; 2 April 2006; A. Schönhofer leg. ● 1 male (ZFMK MYR11332); Thessaly, Kalambaka, Meteora; September 2019; P. Knautt leg. ● 2 males, 1 juvenile (ZFMK MYR11334); same data ● 2 females (NHMW MY10417); Central Greece, Karpenisi; V. Apfelbeck leg. ● 1 female "?type", (ZSM-A20070858), Epirus.

**Remarks.** Attems (1935), although he examined only a few males, already pointed out differences in the telopods between his *australis* and *media*, which we found to be constant after examining more males. The median lobe

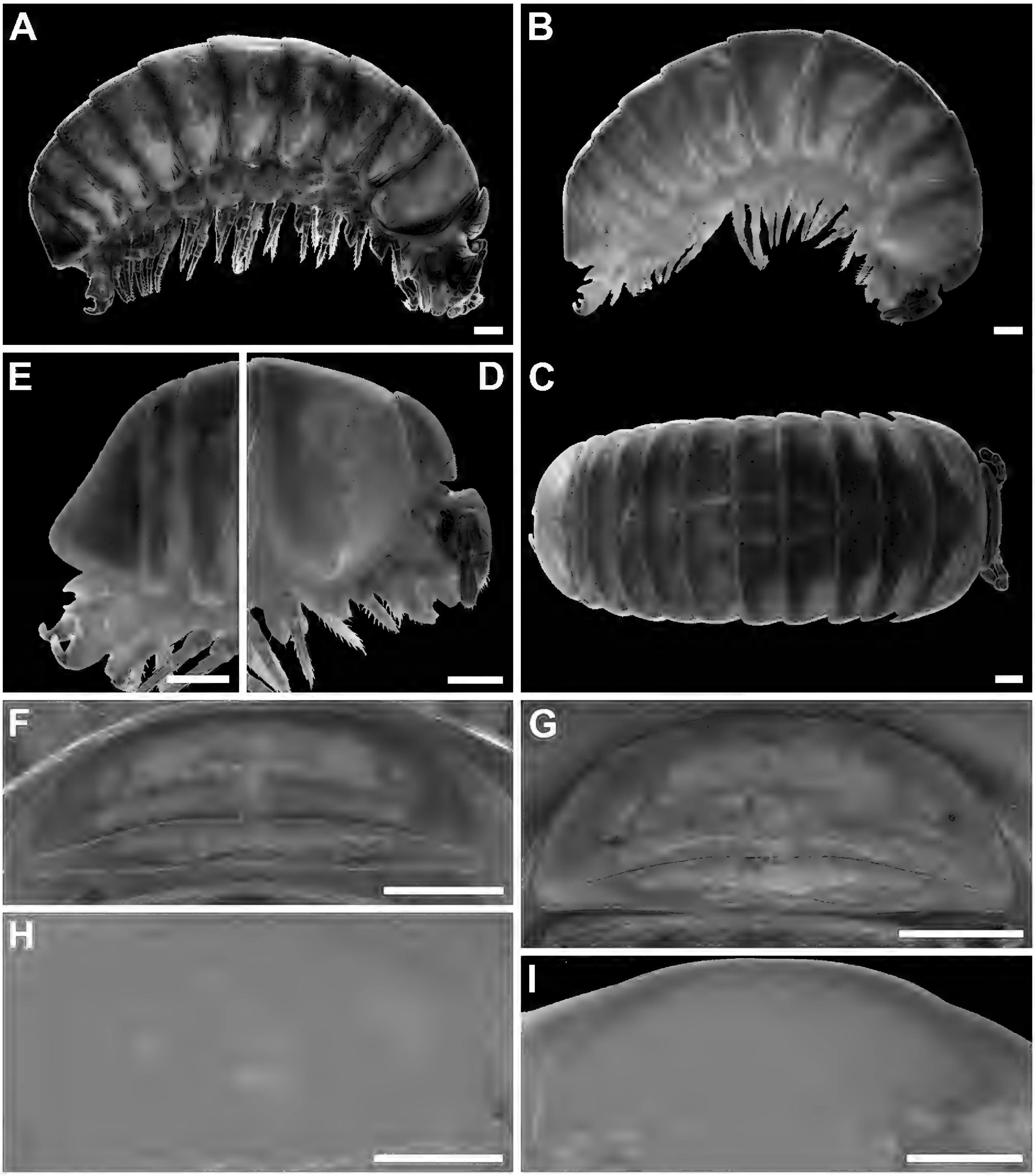


**Figure 8.** *Onychoglomeris australis* Attems, 1935, stat. nov. **A.** Lectotype male (NHMW MY10424), habitus, lateral view; **B–G.** Males from Konitsa, Greece (NHMW MY10420). **B.** Male 1, habitus, lateral view; **C.** Male 1, habitus, dorsal view; **D.** Male 1, anterior part of body, lateral view; **E.** Male 3, anal shield, lateral view; **F.** Male 1, collum, anterior view; **G.** Male 3, collum, anterior view; **H.** Female from Katarraktis, Greece (NHMW MY10419), collum, anterior view; **I.** Male from Katarraktis, Greece (NHMW MY10419), collum, anterior view. Scale bars: 1 mm.

of the syncoxite is high and rounded distally (Fig. 9A, B, D, H) in all but one of the males examined. In one, it is lower and flattened distally (Fig. 9C), which looks more like an anomaly. Attems (1935: 150, fig. 7) also noted a strongly developed conical tooth on the telopoditomere 3 (= tibia). The same was clearly illustrated by Thaler (1999: 199, figs 16, 17). In the males examined by us, this structure is always the same, conical and well developed (Fig. 9A, B, E, white arrows). Such a structure is mentioned for *O. media* stat. nov. by Attems (1935) as much smaller compared to *O. australis* stat. nov. Our observation was the same (see remarks under *O. media* stat. nov.).

As one of the differences, Attems (1935: 150, fig. 6) mentioned the absence of the medial syncoxital lobe of

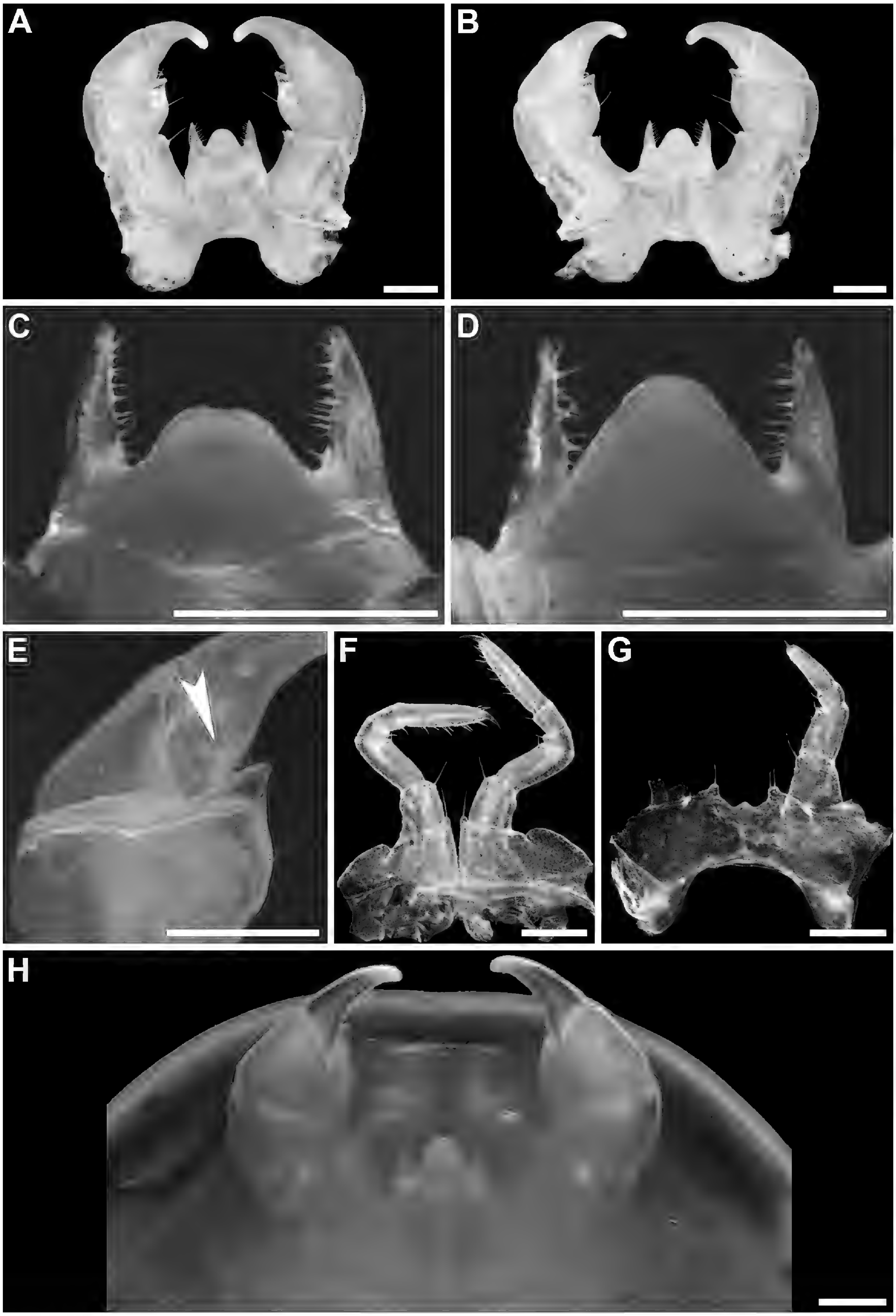


**Figure 9.** *Onychoglomeris australis* Attems, 1935, stat. nov. **A.** Male 4 from Konitsa, Greece (NHMW MY10420), telopods, anterior view; **B.** Male 4 from Konitsa, Greece (NHMW MY10420), telopods, posterior view; **C.** Paralectotype male 1 (NHMW MY3900), telopod syncoxite, posterior view; **D.** Paralectotype male 2 (NHMW MY3900), telopod syncoxite, posterior view; **E.** Male 4 from Konitsa, Greece (NHMW MY10420), part of right telopod, posterior view; **F.** Male 4 from Konitsa, Greece (NHMW MY10420), leg pair 17, anterior view; **G.** Male 4 from Konitsa, Greece (NHMW MY10420), leg pair 18, anterior view; **H.** Male 1 from Konitsa, Greece (NHMW MY10420), leg pair 18 and telopods *in situ*, anterior view. White arrow indicates posterior tooth of telopoditomere 3. Scale bars: 0.5 mm.

leg pair 18 in *O. australis* stat. nov. However, after having checked all males available to us, we conclude that this feature is variable, as some males present this lobe (Fig. 9G). On the other hand, we found that podomere 2 is short and has a straight mesal margin (Fig. 9G, H), as also drawn by Attems (1935: 150, fig. 6), quite different from *O. media* stat. nov. (see Remarks under *O. media* stat. nov.).

In all examined males, the anal shield is predominantly straight in lateral view (Fig. 8A, B), in some only slightly concave (Fig. 8E), but never as distinct as in *O. media* stat. nov. (see below, Fig. 10A). Attems (1935) reported two transverse ridges on the collum. After examining all males and females, we found that this feature is variable and that, in addition to specimens with one (Fig. 8F) or two (Fig. 8H) ridges, there are also those with lateral beginnings of the second ridge (Fig. 8G) or that the second ridge is interrupted only in the centre (Fig. 8I).

We would like to emphasise that juveniles of this species are lighter in colour and are characterised by colour patterns that are not seen or not that obvious in adults and should not be confused with other glomerids from the region (Fig. 12C, D).

The two southernmost finds of this species in Central Greece were apparently misidentified as *G. herzogowinensis* by Verhoeff (1901: 249). Although Verhoeff stated that he had three males from Karpenisi, it is very likely that he did not check the telopods, but made his identification on the basis of the very similar habitus with *G. herzogowinensis*. Unfortunately, we were unable to track down this Verhoeff material. We only found two females in the NHMW collection. As we were unable to look at the males, these two southernmost localities are marked with a question mark on the map.

**Habitat.** From 170 m to 1400 m elev. *Abies*, *Carpinus*, *Quercus*, *Juniperus*, *Pinus*, under stones, under tree trunks, under mossy limestone debris, leaf litter in limestone areas, open areas, bushland.

**Distribution.** Known from Epirus, Thessaly and central Greece (Fig. 13). *Epirus:* Paraskevi on Athamanika (Attems 1935), Buka Chalasmata near Platanoussa (Attems 1935), Katarraktis (Attems 1935), Prosgoli (Verhoeff 1901 [missidentification]; Attems 1935), Graveniti (Strasser 1976), Elati (Strasser 1976), Ligiades (Strasser 1976), Metsovon (Strasser 1976), Filiate (Strasser 1976), Aoos near Konitsa (Thaler 1999), Timfi near Mikropapingo (Thaler 1999), Monodendri - Ano Pedina (present study), Zoodochos Pigi (present study). *Thessaly:* Kastanea, Elafi (present study), Panagia (present study), Kalambaka (present study). *Central Greece:* Karpenisi (Verhoeff 1901 [missidentification]; Attems 1935), Velouchi on Tymfristos (Verhoeff 1901 [missidentification]).

**Type locality.** Paraskevi, Epirus, Greece. Attems (1935: 143) stated: "Paraskevi ist ein Gipfel des Cumerka-Gebirges" which translates that Paraskevi is a summit on the Tzoumerka (= Athamanika) Mountain. We could not find out where exactly Paraskevi is located.

### *Onychoglomeris media* Attems, 1935, stat. nov.

Figs 10, 11, 12E, F

*Onychoglomeris hercegovinensis media* (sic!).– Attems (1935: 149, figs 4, 5).

*Onychoglomeris hercegovinensis* (sic!) in part.– Attems (1929: 289, 312).

*Onychoglomeris herzogowinensis*.– Mauriès et al. (1997: 258–260, fig. 2).

*Onychoglomeris herzegowinensis* (sic!).– Ćurčić et al. (1999: 11P).

*Onychoglomeris herzogowinensis* in part.– Kime and Enghoff (2011: 34, 118).

*Glomeris herzogowinensis*.– Verhoeff (1901: 248).

*Glomeris herzogowinensis* in part.– Verhoeff (1901: 249).

?*Glomeris marginata*.– Sekulić and Živić (2017: 193). [Missidentification, but see Remarks below].

**Diagnosis.** Similar in colouration (Fig. 12E, F) and morphology to the geographically very close *O. australis* stat. nov., but differs in the appearance of the anal shield, leg pair 18 and telopods. Anal shield distinctly concave in lateral view (vs. straight in *O. australis* stat. nov.). Leg pair 18 with podomere 2 longer, twice as long as wide with distinctly convex mesal margin (vs. podomere 2 shorter, ca. 1.5 times longer than wide, with straight mesal margin in *O. australis* stat. nov.). Telopods apparently more robust, with a well-developed posteriomesal process of telopoditomere 2 (= femur) and longer telopoditomere 4 (= tarsus), brownish stripes at the base of posteromesal process of telopoditomere 2 present (vs. absent in *O. australis* stat. nov.), telopoditomere 3 (= tibia) with a poorly developed, sometimes almost absent, posterior tooth that is subtriangular (vs. tooth well developed, conical in *O. australis* stat. nov.), the syncoxite is mostly low, somewhat bilobed (vs. syncoxite usually higher and rounded in *O. australis* stat. nov.). For some more details, see Remarks below.

**Material studied.** ***Lectotype.*** 1 male (NHMW MY3901) in ethanol; Albania, Dukati [= Dukat]; 5 August 1911; A. Winneguth leg. Including two slides: one with telopods, second one with leg pairs 16–18 and right leg 13 or 14. Lectotype here designated.

***Paralectotypes.*** • 2 females (NHMW MY10425); same data as for lectotype; • 1 female (NHMW MY3902); Albania, Kanina [= Kaninë]; November 1908; A. Winneguth leg.

**Other material examined.** Albania: • 1 male, 1 female (NHMW MY10412); Valona [= Vlorë]; Dr. K. Patsch leg.; • 5 males, 2 females (IZB); Gjirocastro [= Gjirokastër]; 10 May, 1973; M. Karaman leg. • 1 male, 2 females (ZFMK MYR13662); Gjirokastër District, Vjosa Valley, Përmet, Strëmbec, hiking trail Ri Soptit Waterfall; forest of low *Carpinus*, *Quercus*, *Platanus* and *Crataegus*, in leaf litter, 40.1488, 20.4543; 6 October 2023; H. Reip leg. Serbia: • 1 male (IZB), slide with a male telopods and leg pairs 17 and 18; Visoki Dečani, Kosovo and Metohija; 1973; M. Karaman leg.

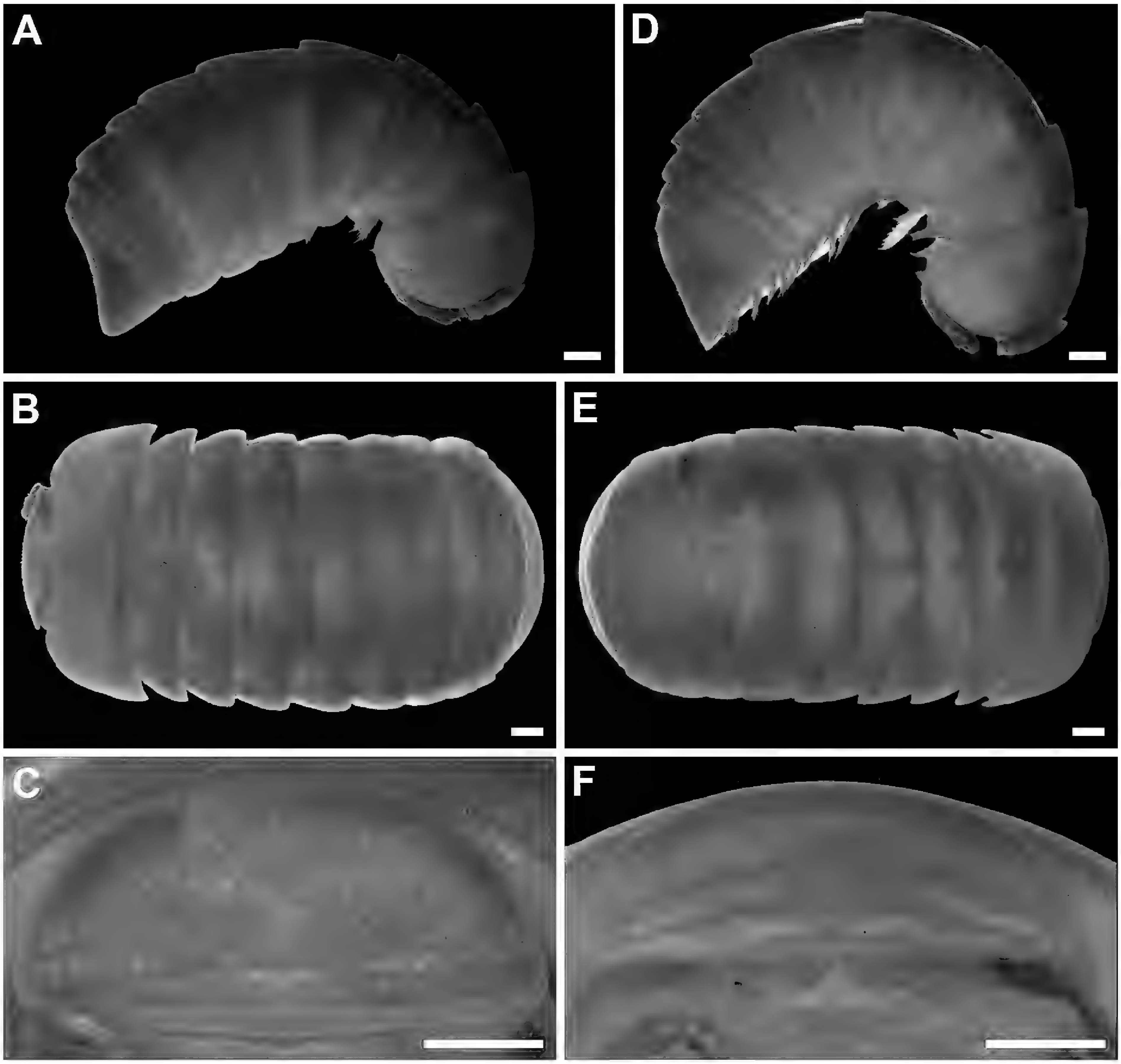


**Figure 10.** *Onychoglomeris media* Attems, 1935, stat. nov., lectotype male (**A–C**, NHMW MY3901) and paralectotype female (**D–F**, NHMW MY10425). **A, D.** Habitus, lateral views; **B, E.** Habitus, dorsal views; **C, F.** Collum, anterior and anterodorsal views respectively. Scale bars: 1 mm.

**Remarks.** As written above, one of the differences between *O. media* stat. nov. and *O. australis* stat. nov. is a much smaller tooth of telopoditomere 3 (= tibia) of the telopods in *O. media* stat. nov. In all males we had, this tooth is poorly developed and sometimes almost absent (Fig. 11D–F, white arrows). This structure was probably overlooked by Mauriès et al. (1997). It is interesting to note that, at the base of the strongly-developed posteromesal process of telopoditomere 2 (= femur), one or more brownish darker stripes were observed in all males available to us (Fig. 11A, C, E, black arrows). Such stripes are absent from all males of *O. australis* stat. nov. at hand. In comparison with *O. australis* stat. nov., podomere 2 of leg pair 18 is longer and has a convex mesal margin that looks somewhat like a blade (Fig. 11B, G). The medial syncoxital lobe of leg pair 18 may be present or absent as in *O. australis* stat. nov. (Fig. 11B, G; see also Mauriès et al. (1997: 259, fig. 2B, F)). All males at our disposal have a distinctly concave anal shield (Fig. 10A). In contrast to Mauriès et al. (1997), who found consistency in Albanian specimens with regard to the presence of only one transverse ridge on the collum, we found it variable as in *O. australis* stat. nov. with one or two complete ridges, sometimes a second only as lateral remains (Fig. 10C, F).

It is of interest to mention a very isolated find in southern Serbia, near Visoki Dečani. This site is almost 250 km by air from the nearest site in the core area of southern Albanian sites (Fig. 13). In the IZB collection, only the microslide with the telopods and the leg pairs 17 and 18 have been found so far and both the telopods and the leg pair 18 fit into the concept of *O. media* stat. nov. Whether it was a mistake

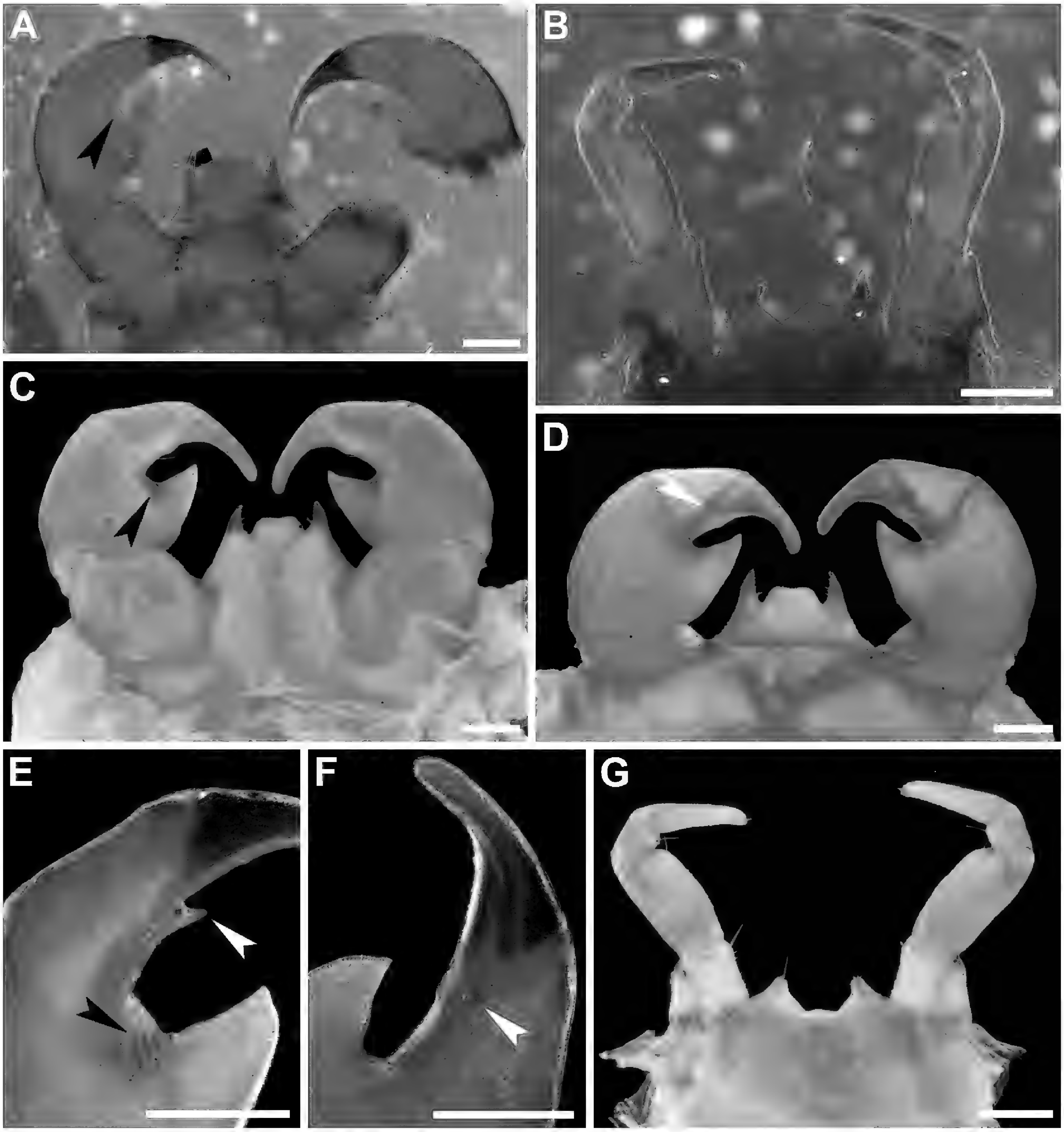


**Figure 11.** *Onychoglomeris media* Attems, 1935, stat. nov. **A.** Lectotype male (NHMW MY3901), telopods, anterior view; **B.** Lectotype male (NHMW MY3901), leg pair 18, anterior view; **C.** Male from Vlorë, Albania (NHMW MY10412), telopods, anterior view; **D.** Male from Vlorë, Albania (NHMW MY10412), telopods, posterior view; **E.** Male from Gjirokastër, Albania (IZB), part of the left telopod, anterior view; **F.** Male from Gjirokastër, Albania (IZB), part of the left telopod, posterior view; **G.** Male from Vlorë, Albania (NHMW MY10412), leg pair 18, anterior view. White arrows indicate posterior tooth on telopoditomere 3, black arrows indicate characteristic brownish stripes of telopoditomere 2. Scale bars: 0.5 mm.

in labelling or the species is really so widespread must be clarified in the future. The latter is supported by the fact that Sekulić and Živić (2017) recorded the occurrence of *Glomeris marginata* in southern Serbia (Znosek, Leposavić), about 80 km north-east of Visoki Dečani. It is obvious that this is not *G. marginata*, but it remains questionable which species Sekulić and Živić (2017) actually found. For the purposes of this paper, we will refer to these two Serbian records as *O. media* stat. nov. with a question mark.

**Habitat.** There is no information about the habitat of this species in the literature, except that Mauriès et al. (1997) mentioned that specimens were found under stones and in leaf litter. Considering the distribution of the species, the habitat should be considered the same as for *G. herzogowinensis* and *O. australis* stat. nov. According to new data, it can be found in *Carpinus*, *Quercus*, *Platanus* and *Crataegus* forest, in leaf litter.

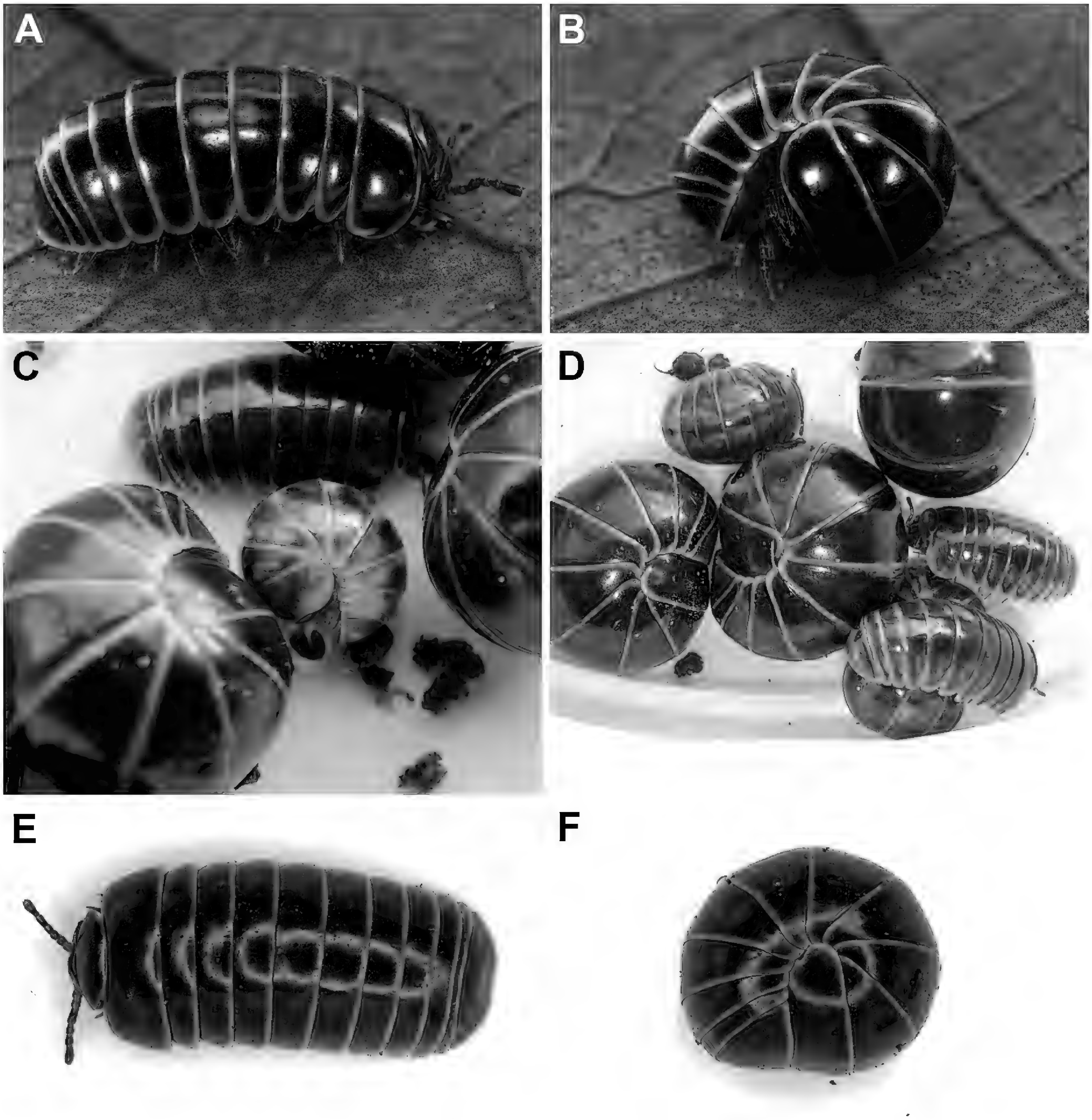


**Figure 12.** Living specimens. **A–D.** *Onychoglomeris australis* Attems, 1935, stat. nov., specimens from Kalambaka, Greece. **E–F.** *Onychoglomeris media* Attems, 1935, stat. nov., specimens from Përmet, Albania. Photos by Morris Fleck (**A, B**), Peter Kautt (**C, D**) and Hans Reip (**E, F**).

**Distribution.** Southern Albanian species with a single, isolated locality in southern Serbia (Fig. 13). Albania: Dukat (Attems 1935; Mauriès et al. 1997), Kaninë (Attems 1935); Vlorë (Verhoeff 1901 [missidentification]; Attems 1929 [missidentification], 1935); Dhërmi (Mauriès et al. 1997), Himarë (Mauriès et al. 1997), Llogara Pass (Mauriès et al. 1997), Gjirokastër (Mauriès et al. 1997; present study), Përmet (present study). Serbia: Visoki Dečani (Ćurčić et al. 1999), ?Leposavić (Sekulić and Živić 2017 [missidentification]).

**Type locality.** Dukat, Vlorë County, southern Albania.

# Discussion

Our DNA barcoding analysis clearly confirms the results of the morphological analysis of the telopods: *Glomeris herzogowinensis* groups with other *Glomeris* species and not with *Onychoglomeris*, while *O. australis* stat. nov. clearly groups with *Onychoglomeris*. Interestingly, the sister species to *G. herzogowinensis* seems to be *G. maerens* from Spain, a similarly-coloured species living in a similar Mediterranean habitat. However, there are indications that more than one species is currently hiding

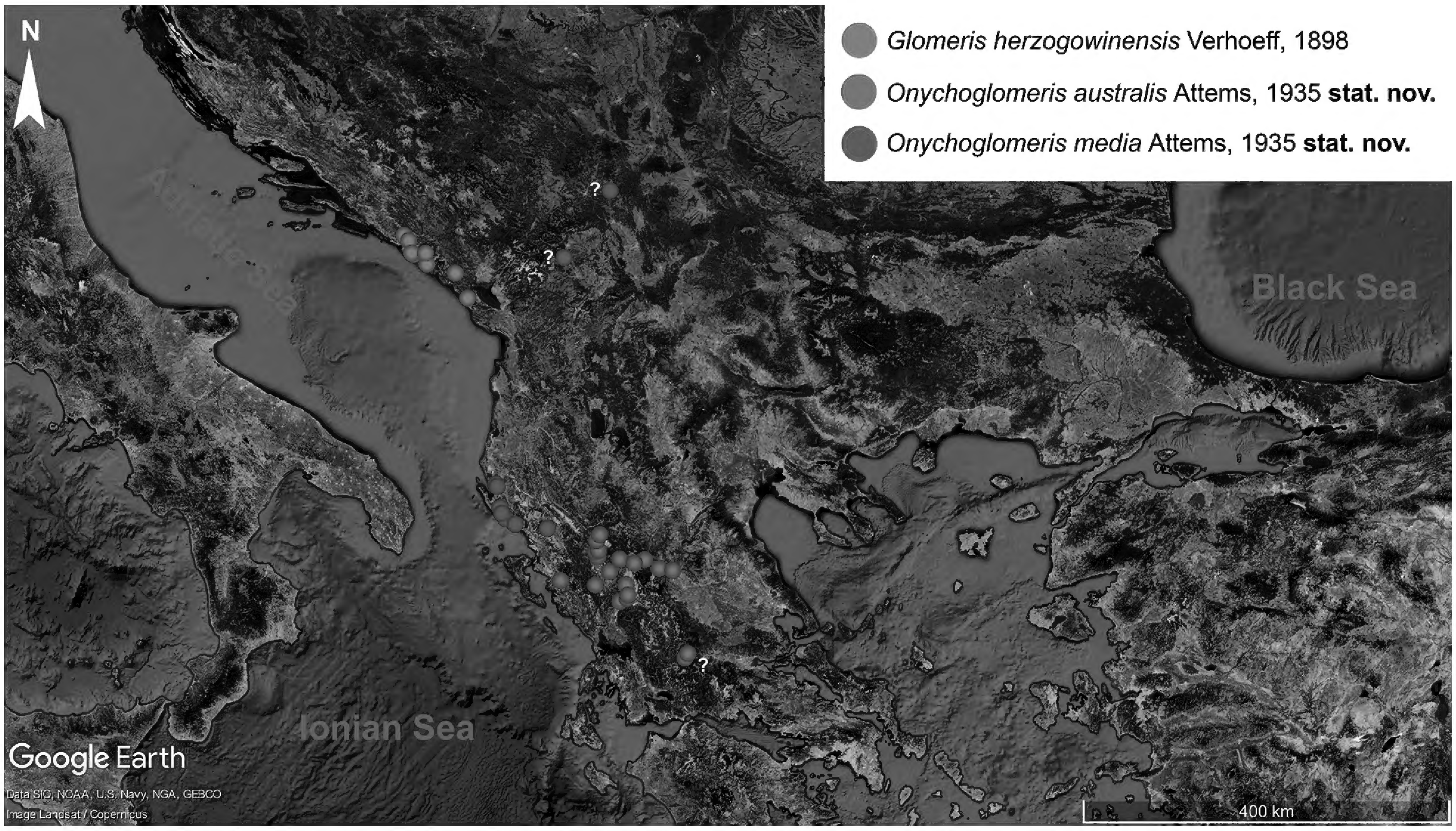


**Figure 13.** Distribution map of *Glomeris herzogowinensis* Verhoeff, 1898, *Onychoglomeris australis* Attems, 1935, stat. nov. and *Onychoglomeris media* Attems, 1935, stat. nov.

under the name *G. maerens* (Reip and Wesener 2018). The observed genetic distances of the COI barcoding gene between *G. herzogowinensis* and other *Glomeris* species, as well as those between *O. australis* stat. nov. and other *Onychoglomeris*, are with 11–16% similarity to interspecific distances found in other barcoding studies of species of the family Glomeridae (Wesener and Conrad 2016; Kuroda et al. 2022; Recuero and Caterino 2023), but lower than those observed in the diverse genus *Trachysphaera* Heller, 1858 (Wilbrandt et al. 2015). The interspecific distances observed here fit well within the range observed in millipedes from other taxonomic groups and other geographic areas, such as the related (Oeyen and Wesener 2018) giant pill-millipedes (order Sphaerotheriida) from Madagascar (Wesener et al. 2014; Wesener and Sagorny 2021) and southeast Asia (Wesener 2019; Bhansali and Wesener 2022) or in Spirobolida from Madagascar (Wesener et al. 2011; Wesener 2020) and Thailand (Pimvichai et al. 2020, 2022).

This work represents another example demonstrating the importance of natural history collections as a timeless resource allowing us to study organisms and their systematics, sometimes even discover and describe completely unknown taxa, awaiting on shelves of museums to be determined, described and documented. The average shelf-life of all kinds of species of living organisms was estimated to be around 20.7 years (see Fontaine et al. (2012)) with extreme cases exceeding 100 years like *Pleonopurus tanzanicus* Enghoff & Akkari, 2022 and reaching as high as 149 years such as *Ommatoiulus schubarti* Akkari & Enghoff, 2012 (Akkari and Enghoff 2012; Enghoff and Akkari 2022). In other cases, taxa have inadevertedly been mixed with other hitherto described species, therefore remaining hidden for decades. One of the latest examples is perhaps that of *Lophostreptus neglectus* Enghoff & Akkari, 2024 discovered amongst the syntypes of its congener *Lophostreptus regularis* Attems, 1909 in two different collections in Sweden and Vienna and described more than a century after it was originally collected (Enghoff and Akkari 2024). The scientific collections, especially type series and historical specimens, are most defintely an invaluable source of information for taxonomists to update information, unravel the identity of obscure historical names (e.g. Akkari et al. (2010); Akkari (2013); Antić and Akkari (2020); Antić et al. (2021)), clarify the taxonomic status of taxa and solve complicated riddles like the one presented in this work. Morphology-based taxonomy remains a subjective exercise, especially when the studied groups did not traditionally have well-defined characters for species characterisation, which is the case for the order Glomerida. Taxonomy is also very prone to human error and this has been illustrated in numerous cases, especially in times when a tremendeous amount of taxa had to be described by a generation of taxonomists who did not enjoy the same advantages of communication means and technological facilities, not the least microscopy. Amending these mistakes and updating the nomenclature of taxa, adding pieces of knowledge on their genetic information remains an ongoing process that make us acknowledge the colossal work accomplished by myriapod experts like Attems and Verhoeff, but also humble us once we also think towards the future and what could be achieved in perhaps less time given the same resources and further technological progress.

In this article, we tried to solve the case of three species that have been hidden under the same name. *Glomeris herzogowinensis* was confirmed as an unquestionably good taxon. We have raised the other two taxa of the genus *Onychoglomeris*, former subspecies, to species level. Considering the fact that we have no genetic data for *O. media* stat. nov. and that both *O. media* stat. nov. and *O. australis* stat. nov. very likely occur sympatrically at least in the Vjosa (in Albanian) or Aoos (in Greek) river valley in southern Albania and north-western Greece, respectively, some might disagree with such an act. In this context, and due to some morphological differences that obviously exist, we believe that the Albanian and Greek populations should be treated as separate species for the time being.

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# Supplementary material 1

## Number of base differences per site (*p*-distances) between sequences

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Data type: xls



Link: https://doi.org/10.3897/zse.100.122288.suppl1